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Original Article

Predictable hydrodynamic conditions explain temporal variations in the density of benthic foraging seabirds in a tidal stream environment

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Tidal stream turbines could have several direct impacts upon pursuit-diving seabirds foraging within tidal stream environments (mean horizontal current speeds $> 2\,ms^{-1}$), including collisions and displacement. Understanding how foraging seabirds respond to temporally variable but predictable hydrodynamic conditions immediately around devices could identify when interactions between seabirds and devices are most likely to occur; information which would quantify the magnitude of potential impacts, and also facilitate the development of suitable mitigation measures. This study uses shore-based observational surveys and Finite Volume Community Ocean Model outputs to test whether temporally predictable hydrodynamic conditions (horizontal current speeds, water elevation, turbulence) influenced the density of foraging black guillemots *Cepphus grylle* and European shags *Phalacrocorax aristotelis* in a tidal stream environment in Orkney, United Kingdom, during the breeding season. These species are particularly vulnerable to interactions with devices due to their tendency to exploit benthic and epi-benthic prey on or near the seabed. The density of both species decreased as a function of horizontal current speeds, whereas the density of black guillemots also decreased as a function of water elevation. These relationships could be linked to higher energetic costs of dives in particularly fast horizontal current speeds ($>3\,ms^{-1}$) and deeper water. Therefore, interactions between these species and moving components seem unlikely at particularly high horizontal current speeds. Combining this information, with that on the rotation rates of moving components at lower horizontal current speeds, could be used to assess collision risk in this site during breeding seasons. It is also likely that moderating any device operation during both lowest water elevation and lowest horizontal current speeds could reduce the risk of collisions for these species in this site during this season. The approaches used in this study could have useful applications within Environmental Impact Assessments, and should be considered when assessing and mitigating negative impacts from specific devices within development sites.

Keywords: *Cepphus grille*; environmental impacts; foraging ecology; FVCOM; *Phalacrocorax aristotelis*; shore-based surveys; tidal stream turbines.

Introduction

Tidal stream turbine installations will place novel anthropogenic structures into habitats characterized by mean horizontal current speeds exceeding $2\,ms^{-1}$ (Fraenkel, 2006). These installations could have several impacts upon pursuit-diving seabirds exploiting these tidal stream environments (Furness *et al.*, 2012), and these impacts could span many spatial and temporal scales (Scott *et al.*, 2014). However, impacts within the areas immediately around installations ($<1\,km^2$) generally cause most concern, as these will have the most direct effects upon local populations (Furness *et al.*, 2012). In particular, pursuit-diving seabirds may either avoid areas near moving components resulting in displacement from foraging areas (Langton *et al.*, 2011) and/or collide with moving components resulting in serious injury or mortality (Wilson *et al.*, 2007). Installations will also change near-field hydrodynamics through the removal of tidal stream energy and the alteration of current regimes, with possible consequences on foraging opportunities and efficiency (Shields *et al.*, 2011). Addressing these concerns requires a detailed understanding of a species foraging behaviours in the areas immediately around the potential locations of devices (Waggitt and Scott, 2014). Intensive studies focussing upon areas of high horizontal current speeds are essential for this understanding, as foraging behaviours observed within these areas are likely to be very different to those within more benign areas. These differences in behaviour are likely to be driven by the unique physical characteristics of the former (Benjamins *et al.*, 2015). However, few studies have investigated a species foraging behaviours within very specific areas ($< 1\ km^2$) (Heithaus, 2005; Watanuki *et al.*, 2008), and none have focussed on areas of high horizontal current speeds.

Within the United Kingdom, black guillemots *Cepphus grylle* and European shags *Phalacrocorax aristotelis* are considered particularly vulnerable to interactions with installations due to their tendency to exploit benthic and epi-benthic prey on or near the seabed (Furness *et al.*, 2012). Predictable but temporally variable hydrodynamic conditions, varying systematically across ebb-flood tidal cycles, could influence benthic foragers' use of particular areas. For instance, seabirds may exploit times of faster horizontal currents to cover larger seabed areas or track epi-benthic fish as they are washed downstream (Holm and Burger, 2002; Robbins *et al.*, 2014). Seabirds could also exploit times of high turbulence, originating from interactions between fast horizontal currents and bathymetry, when three-dimensionally complex motions could flush benthic and epi-benthic prey into open water and/or restrict their anti-predatory responses (Benjamins *et al.*, 2015; Hunt *et al.*, 1999). However, on the other hand, seabirds could avoid times of particularly high horizontal current speeds, extreme turbulence or deeper water elevation (e.g. high tides) due to the increased energetic costs of performing foraging dives in these hydrodynamic conditions (Butler and Jones, 1997; Heath and Gilchrist, 2010). Therefore, benthic foragers' temporal use of a particular area could be synergistically influenced by prey exploitability and dive performance, with individuals showing trade-offs between the ease of capturing prey and the energetic cost of performing dives (Davies *et al.*, 2012). Understanding how foraging black guillemots and European shags respond to temporally predictable hydrodynamic conditions around the potential locations of devices would identify times when interactions between seabirds and moving components are most likely. This information would help to both quantify the magnitude of any direct impacts, and also facilitate the development of suitable mitigation measures. Such information could also predict whether changes in near-field hydrodynamic processes could affect foraging opportunities and efficiency.

This study investigates how temporally predictable hydrodynamic conditions influenced the density of foraging black guillemots and European shags immediately around the potential location of a tidal stream turbine installation in Orkney, United Kingdom ($<1\,km^2$). Specifically this study asks whether: (i) the density of foraging black guillemots and European shags varied significantly as a function of horizontal current speeds, turbulence or water elevation, and (ii) any relationships with hydrodynamic conditions differed between these species, indicative of interspecific variations in foraging strategies. Addressing such questions requires particular areas to be monitored intensively across multiple ebb-flood tidal cycles, recording concurrent behavioural and hydrodynamic datasets at a fine temporal resolution (minutes). These datasets are usually collected from research vessels using observational surveys and deployments of oceanographic instruments (Embling *et al.*, 2012; Scott *et al.*, 2013). However, the prolonged presence of research vessels within a particular area could strongly influence the behaviour of foraging seabirds, possibly leading to unrepresentative conclusions (Schwemmer *et al.*, 2011). However, in coastal environments, a combination of shore-based observational surveys and Finite Volume Community Ocean Model (FVCOM) outputs (Chen *et al.*, 2003) overcomes these issues by recording seabird behaviours from adjacent coastlines, and quantifying hydrodynamics from computational studies. This study therefore uses such an approach to answer the aforementioned questions. Results are then discussed with regard to the physical influences of temporal variations in foraging activity, and to the environmentally sustainable operation of tidal stream turbines.

Methods

Data collection

This study was performed within the Fall of Warness (hereafter FOW: 57°7′–57°11′N, 002°47′–002°50′W), Orkney, United Kingdom over 13 days between 21 May and 2 June 2013, coinciding with the black guillemot and European shag breeding season. The FOW is an active tidal stream turbine test site managed by the European Marine Energy Centre (EMEC), and is characterized by numerous locations which are suitable for devices (mean horizontal current speeds $> 2\,ms^{-1}$). The study area covered one of these locations, spanning approximately $0.70\,km^2$ near the Seal Skerry headland in the northern sector of the FOW (Figure 1). However, whilst there can be up to eight devices located across the test site, no devices have ever been deployed in the study area; the nearest berth is located ~500 m to the south of the study area.

Tidal terminology

Within coastal environments there is typically a temporal mismatch between times of highest and lowest water elevation and those of lowest horizontal current speeds, which could create confusion when describing tidal states. Therefore, the following terminology will be used in this study: (i) 'high tide' and 'low tide' describe periods of highest and lowest water elevation, respectively, (ii) 'flood tide' and 'ebb tide' describe periods when water elevation is steadily increasing and decreasing, respectively, and

Figure 1. Studies were performed in the Fall of Warness, Orkney, UK. The study area was 0.5–2 km to the south-west of the Seal Skerry headland. The location of Orkney and Seal Skerry is shown by a square and circle respectively. The vantage point and area used in shore-based observational surveys to record the abundance and behaviour of seabirds is shown by a triangle and hatched polygon, respectively.

(iii) 'high-slack tide' and 'low-slack tide' describe periods when horizontal current speeds are at their lowest, with the former indicating that this period is closer to high tide, and the later indicating that this period is closest to low tide.

Seabird distributions

Shore-based observational surveys were used to record the abundance and behaviour of black guillemots and European shags on the sea surface within the study area. A suitable vantage point was located on the Seal Skerry headland (59°10.295′N, 002°49.391′W: Figure 1) ~5 m above mean sea level and ~0.5–1.5 km away from the study area. Having a vantage point <2 km from the study area assured that all seabirds on the sea surface could be identified to species level, detailed behavioural observations could be performed, and variations in detectability associated with distance and sea surface conditions would be minimized (Waggitt *et al.*, 2014). Scans were only performed when the sea state was <Beaufort scale 3, and visibility was >1.5 km. No more than 4 h of surveys were performed in a day, to reduce the effects of observer fatigue.

Shore-based surveys consisted of either 10 or 20 min scans; 88 scans of 10 min length and 37 scans of 20 min length were performed over a total of 27 hr. The number of scans performed per day averaged 9.54, and varied from 0 to 21. The differing scan lengths represented the use of two slightly different scanning strategies which were being tested. Attempts were made to perform equal amounts of scans across different combinations of tidal state and time of day (*ToD*), therefore accounting for possible diurnal patterns in foraging activities. However, extended bouts of poor weather during surveys meant that hours around high tide were covered considerably less than others (Table 1), whereas coverage of morning (04:00–12:00 GMT) and afternoon (12:00–20:00 GMT) periods were biased to flood and ebb tides, respectively (Table 2). Nevertheless, there were still many scans performed in hours around high tide ($n = 8$, 2.27 hr), and also for under-sampled tidal states in both morning (Ebb: $n = 14$, 2.83 h) and afternoon (Flood: $n = 28$, 5.5 hr) periods. As surveys only spanned 13 days, potential changes in foraging activity linked with reproductive duties (Ito *et al.*, 2010) were likely to be negligible. Therefore, the potential influence of reproductive duties was not given consideration when designing the survey schedule.

Table 1. Number (No) and duration (hr) of scans performed during shore-based observational surveys per hour of the ebb-flood tidal cycle between 21 May and 2 June 2013 near Seal Skerry, Orkney, UK.

Hours after high tide	No	hr
0–1	4	1.17
1–2	9	2.17
2–3	11	2.67
3–4	12	2.83
4–5	11	2.00
5–6	8	1.67
6–7	13	2.83
7–8	15	3.33
8–9	17	3.17
9–10	12	2.50
10–11	9	1.67
11–12	4	1.00

Table 2. Number (No) and duration (hr) of scans performed during shore-based observational surveys per tide state and time period between 21 May and 2 June 2013 near Seal Skerry, Orkney, UK.

	Ebb		Flood	
Time period (GMT)	No	hr	No	hr
04:00–12:00	14	2.83	42	9.00
12:00–20:00	41	9.66	28	5.50

During each scan, the abundance of foraging seabirds across the study area was recorded. All scans were performed in a systematic and repeatable manner using a Swarovski ATS80 telescope at between 25 and 50 times magnification. The observer scanned the area from west to east during south-easterly flows, and vice versa during north-westerly flows. By scanning in the opposite direction to the prevailing current, the observer reduced the probability of counting the same seabird multiple times as

they drifted downstream. The speed of scans was carefully controlled to ensure that they lasted exactly 10 or 20 min. Upon sighting a seabird on the sea surface, the observer watched them until their behaviour could be confidently defined as either foraging or non-foraging. Foraging seabirds were deemed to be those that were either seen diving, or showing evidence of searching behaviours i.e. frequently dipping their head beneath the water surface. During 10 min scans seabirds were watched for up to 1 min, whereas during 20 min scans they were watched for up to 2 min. However, there were no large differences between scans lengths with regard to the proportions of black guillemots (10 min = 0.44 and 20 min = 0.39) or European shags (10 min = 0.77 and 20 min = 0.78) that were detected and subsequently recorded as foraging seabirds. Therefore, the detection of foraging seabirds was not enhanced by the performance of longer scans.

Hydrodynamic conditions

FVCOM (Chen *et al.*, 2003) outputs were used to quantify temporal variances in horizontal surface current speeds (ms^{-1}: *HSpd*), turbulence (horizontal eddy viscosity in $m^2\ s^{-1}$: *Visc*), and water elevation (m: *Elev*) within the study area. The model domain was centred on the FOW, although to minimize open boundary effects it extended to the continental shelf break along the 100 m depth contour. In total, there were 160 000 cells covering ~40 000 km^2. Cell resolution varied smoothly from 5 × 5 km along the continental shelf break, to 100 × 100 m within the FOW. Bathymetry data at 2 × 2 km resolution from the Proudman Oceanographic Laboratory Coastal Ocean Modelling System (Holt *et al.*, 2007) were used across most of the model domain, although multibeam sonar derived bathymetry data at 5 × 5 m resolution from the Maritime and Coastguard Agency (MCA) were used in the FOW. The model was forced at the surface with 7 × 7 to 12 × 12 km resolution weather data from the Met Office Unified Model (Davies *et al.*, 2005) which were interpolated to the cells. At the open boundaries, the model was forced by a surface elevation time series predicted from TPXO harmonics (Egbert *et al.*, 1994). Mean values of hydrodynamic conditions across the study area were provided at 15-min resolution throughout the study period. For each scan which was performed, mean (*Elev*, *Visc*) and maximum (*HSpd*) values of hydrodynamic conditions were sourced from the time interval matching the start of the scan. If this time interval was not available, then values were sourced from the subsequent time interval which was closest to the start of the scan.

Observer effort

In tidal stream environments, the ability of observers to detect seabirds on the sea surface is influenced by variations in *HSpd* (Robbins *et al.*, 2015). The sea surface area passing the observer per time-unit increases when *HSpd* increases, which potentially brings larger numbers of seabirds into the view of the observer i.e. it increases their detectability. To account for these variations in detectability, the number of seabirds recorded within a single scan needs to be adjusted by calculating the total sea surface area that the observer effectively covered within that scan. The abundance of seabirds on the sea surface can then be quantified as a density per area-unit. In this study, the total sea surface area covered by the observer per scan (*EF*) was a function of the extent of the study area, *HSpd*, and the length of the scan. *EF* (km^2) was calculated using formula 1 whereby *Area* was 0.70 km^2, *HSpd* was the corresponding value of *HSpd* converted into km^{-1}, and *Scan* was the length of the scan in seconds. These calculations of EF accounted for the larger sea surface areas that would have been covered in scans performed during times of fast *HSpd* and also the larger sea surface areas covered in scans lasting 20 min.

$$EF = Area * (HSpd * Scan) \quad (1)$$

Analysis

Generalized additive mixed effect models (GAMMs) with Poisson distributions were used to test for relationships between the density of foraging seabirds and hydrodynamic conditions. Models were run for each species. The abundance of foraging seabirds was the response variable with *HSpd, Visc* and *Elev* as the explanatory variables. *ToD* (decimal time) and sea state (*SeaSt*: Beaufort scale) were also included as explanatory variables to account for diurnal rhythms in foraging activities, and potential impacts of sea surface roughness on detectability of seabirds on the sea surface, respectively. Although the detectability of seabirds is also positively affected by flock size, black guillemots (mean group size = 1.05 ± 0.23) and European shags (mean group sizes = 1.00 ± 0.00) were almost always seen foraging alone whereas multi-species foraging aggregations never occurred (a species list is provided in Supplementary Material S1). *HSpd, Visc, Elev and ToD* were modelled as non-linear continuous variables, and smoothing parameters were estimated using maximum likelihood methods. The number of knots for each explanatory variable was fixed at five. Restricting the number of knots at five avoided model overfitting, and helped with the ecological interpretation of results. *SeaSt* was modelled as a linear and continuous variable. *EF* (km^2) was used as a statistical offset to account for variations in the extent of the sea surface area which was covered among scans. A time interval of 1 h was used as a random effect to account for temporal variations in the density of foraging seabirds not explained by hydrodynamic conditions (e.g. weather conditions influencing detectability), and also temporal autocorrelation. This length was selected after inspection of residuals from models without a random effect, which revealed temporal autocorrelation at a scale of ~1 hr. GAMM were performed in R (version 3.1.1, R Development Core Team 2014) using the 'mgcv' (Wood, 2006) package.

Backwards model selection was performed, and only statistically significant ($P < 0.05$) explanatory variables were retained in the final model (Zuur *et al.*, 2009). Plots of residuals showed no evidence of extreme temporal autocorrelation or heterogeneity, and plots of residuals associated with random effects resembled normal distributions (Supplementary Material S2). The relative influence of each significant explanatory variable was assessed by illustrating response curves. Within the calculation of response curves, the explanatory variable of interest was varied between its minimum and maximum values, other explanatory variables were fixed at their median values, and *EF* was fixed at 0.70 km^2. By using an offset of 0.70 km^2, which was the spatial extent of the study area, the values shown within these calculations would represent the densities of foraging birds which would be seen in an instantaneous scan of the study area.

Results

Hydrodynamic conditions

FVCOM outputs showed large variations in hydrodynamic conditions across the study period (Figure 2). Values of maximum

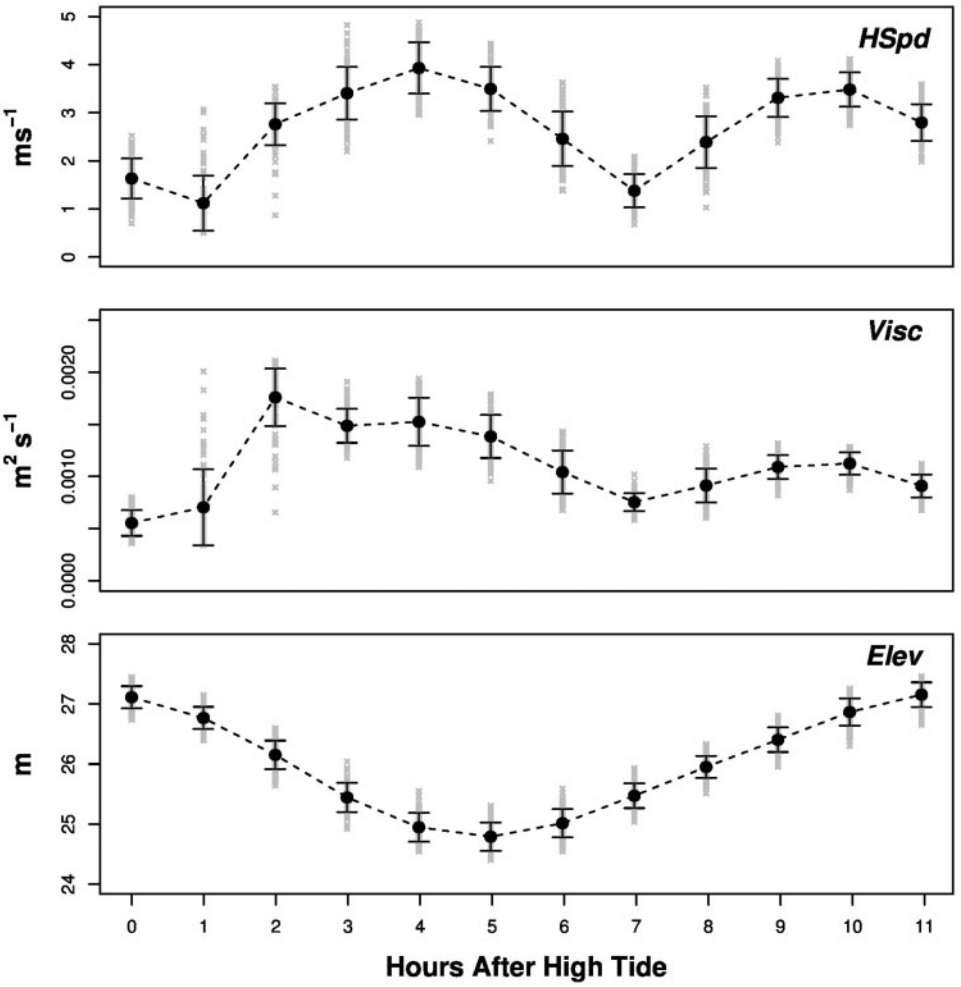

Figure 2. Variations in maximum *HSpd*, mean *Visc* and mean *Elev* across the ebb-flood tidal cycle between 21 May and 2 June near Seal Skerry, Orkney, UK. Values were available at 15-min time intervals. Points and error bars illustrate the mean and standard deviation across all 15-min time intervals, whereas crosses illustrate values from each individual 15-min time intervals. *HSpd* shows horizontal current speeds, *Visc* shows horizontal eddy viscosity and *Elev* shows water depth. Hydrodynamic conditions were quantified using FVCOM outputs.

HSpd varied between 0.52 and 4.88 ms^{-1}, mean *Elev* varied between 24.40 and 27.46 m, and mean *Visc* varied between 0.0003 and 0.0021 m^2 s^{-1}. There were clear temporal mismatches between the times of slack water and the times of high/low water elevation within ebb-flood tidal cycles. Within a cycle, the slowest *HSpd* values (representing slack water) were around 2 hr after the highest and lowest *Elev* values (representing high and low tide, respectively). Similarly, the fastest *HSpd* values were approximately 1 hr before the highest and lowest *Elev* values. Finally, several asymmetries between ebb and flood tides were also present. Peak *HSpd* values were ~1.00 ms^{-1} higher during ebb than flood tides, and peak *Visc* values were also ~0.0007 m^2s^{-1} higher during ebb than flood tides. Flood tides were ~30 min longer than ebb tides.

Black guillemots

The mean density of foraging black guillemots varied considerably across each hour of the ebb-flood tidal cycle, ranging from 0.00 to 1.51 foraging seabirds per km^2. Mean densities of foraging black guillemots peaked between 4 and 8 h after high tide, coinciding with periods around low tide and low-slack tide (Figure 3). Accordingly the density of foraging black guillemots showed significant negative relationships with *HSpd* ($n = 125$, df = 1, $\chi^2 = 10.39$, $P < 0.001$) and *Elev* ($n = 125$, df = 1, $\chi^2 = 34.65$, $P < 0.001$). The effect of *HSpd* and *Elev* could be considered as particularly and moderately strong, respectively; response curves showed densities that were 17.90 times greater for the lowest than the highest *Elev* values, and 4.24 times greater for the lowest than the highest *HSpd* values (Figure 4). The density of foraging black guillemots also showed significant positive relationships with *ToD* ($n = 125$, df = 1, $\chi^2 = 6.18$, $P = 0.01$), indicating that densities were higher during afternoon periods. The effect of *ToD* could be considered as moderately strong; response curves showed densities that were 2.62 times higher for late evening than early morning (Figure 5). The density of foraging black guillemots showed no significant relationships with *SeaSt*.

European shags

The mean density of foraging European shags varied considerably across each hour of the ebb-flood tidal cycle, ranging from 0.21 to 1.73 foraging seabirds per km^2. Mean densities of foraging

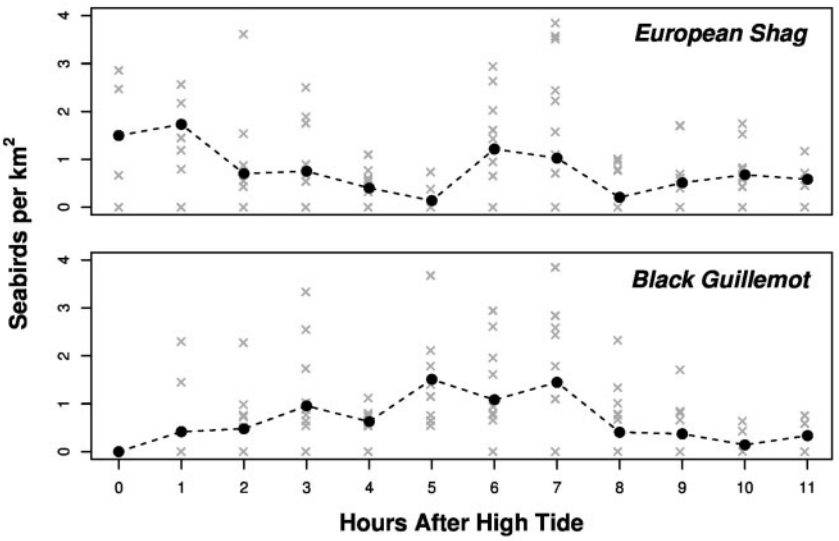

Figure 3. Densities of foraging black guillemots and European shags per hour of the ebb-flood tidal cycle, between 21 May and 2 June near Seal Skerry, Orkney, UK. Points illustrate mean densities recorded across all scans, whereas crosses illustrate densities recorded from each individual scan.

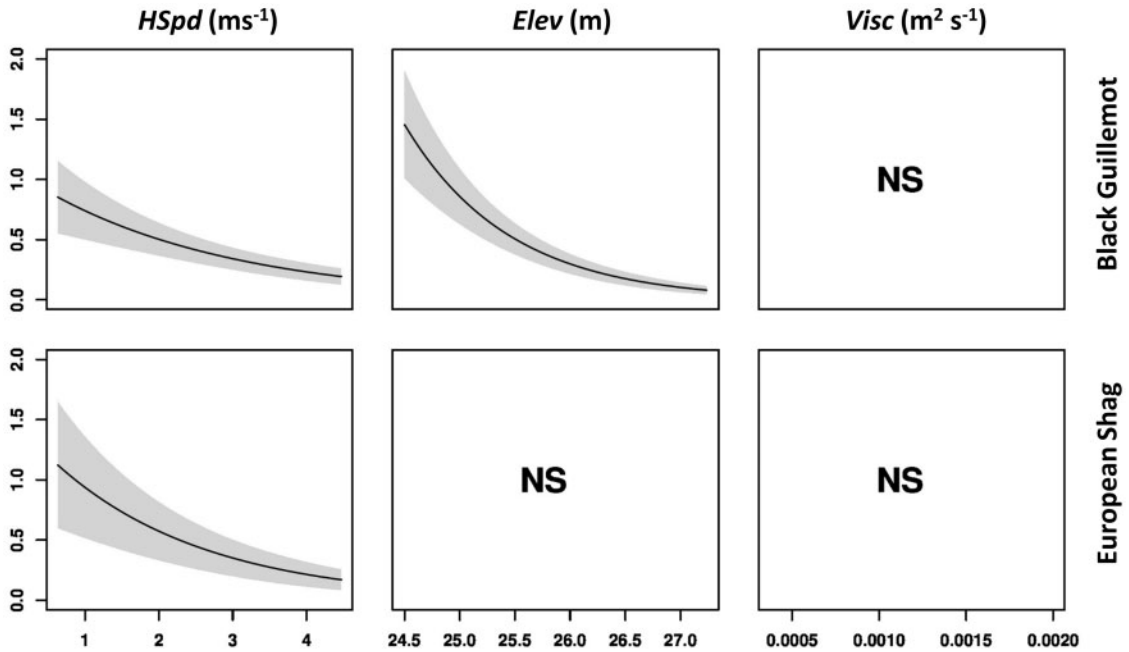

Figure 4. Response curves (± SE) from GAMMs showing predicted densities of foraging black guillemots and European shags as a function of maximum HSpd, mean Elev, and mean Visc near Seal Skerry, Orkney, UK. HSpd represents horizontal current speeds, Visc represents horizontal eddy viscosity and Elev represents water depth. NS, non-significant.

European shags peaked at around 1–2 and 7–8 hr after high tides, coinciding with periods of low- and high-slack tides (Figure 3). Accordingly, the density of foraging European shags showed significant negative relationships with *HSpd* ($n = 125$, $df = 1$, $\chi^2 = 15.42$, $P < 0.001$). The effect of *HSpd* could be considered as moderately strong; response curves showed densities which were 6.55 times greater for the lowest than the highest *HSpd* values (Figure 4). The density of foraging European shags showed no significant relationships with either *ToD* or *SeaSt*.

Discussion

This study investigated how temporally variable but predictable hydrodynamic conditions influenced the density of foraging black guillemots and European shags immediately around the potential location of a tidal stream turbine installation ($<1\,km^2$) in Orkney, United Kingdom. Results indicated that densities of foraging black guillemots and European shags decreased as a function of increased horizontal current speeds, whereas the densities of black guillemots also decreased as a function of increased water

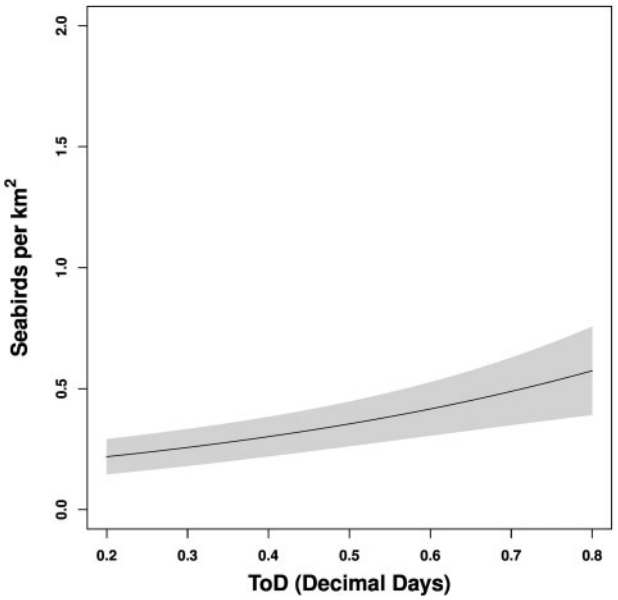

Figure 5. Response curves (± standard error) from GAMMs showing predicted densities of foraging black guillemots as a function of ToD near Seal Skerry, Orkney, UK.

elevation. These relationships manifested themselves in clear patterns of foraging activity across the ebb-flood tidal cycle which differed between species; the highest densities of European shags occurred around low-slack and high-slack tide whilst the highest densities of black guillemots occurred between low-slack and low tide. The hydrodynamic conditions influencing species foraging activities, and also site occupancy patterns, are discussed below. The implications of these findings for predicting impacts immediately around devices, and also developing suitable mitigation measures, are then discussed in more detail.

Hydrodynamic conditions

Associations between foraging seabirds and predictable physical conditions typically concern prey characteristics, with particular hydrodynamic (Benjamins *et al.*, 2015; Hunt *et al.*, 1999) or seabed features (Watanuki *et al.*, 2008) being characterized by dense and exploitable aggregations of prey items. It also seems possible that the longer and deeper dives associated with the exploitation of prey on the seabed (Elliott *et al.*, 2009) could result with benthic foraging species showing additional associations with physical conditions suspected to influence the performance of dives (Butler and Jones, 1997; Heath and Gilchrist, 2010). Both black guillemots and European shags showed associations with hydrodynamic conditions suspected to influence the performance of dives (low horizontal current speeds and/or low water elevation), providing a rare example of diving constraints seemingly effecting the foraging activities of pursuit-diving seabirds (Ronconi and Clair, 2002). In contrast, neither species showed associations with hydrodynamic conditions believed to increase the availability of mobile benthic and epi-benthic prey items (high turbulence and horizontal current speeds). This absence suggests that these species may exploit sessile benthic prey within the study site. Alternatively, levels of turbulence and horizontal currents considered to be low in the study site, but still relatively high in comparison to other habitats, could have been sufficient enough to promote prey availability. In either case, these associations reaffirm that prey availability not only concerns the ease of capturing prey items within the water column, but also the energetic costs required to reach these prey items (Chimienti *et al.*, 2014).

Although both black guillemots and European shags showed associations with hydrodynamic conditions suspected to influence the performance of dives, the identity and strength of associations differed among species; European shags were moderately associated with slower horizontal current speeds, whereas black guillemots were moderately and strongly associated with slower horizontal current speeds and lower water elevation, respectively. Black guillemots and Europeans shags have fundamentally different diving behaviours, the latter being foot-propelled and the former being primarily wing-propelled pursuit-divers (Lovvorn *et al.*, 2001). This is believed to represent trade-offs between manoeuvrability and speed; foot-propelled pursuit-divers typically detect and ambush prey at close range whilst wing-propelled pursuit-divers chase prey in open water (Watanuki *et al.*, 2008; White *et al.*, 2007). These species also have fundamentally different diving physiology, with European shags' larger body size (1.9 kg vs. 420 g) (Snow and Perrins, 2004), partially wettable plumage (Grémillet *et al.*, 2005) and more streamlined morphology (Lovvorn *et al.*, 2001) likely to make the energetic costs of dives comparatively lower than black guillemots (Wanless *et al.*, 1993; Halsey *et al.*, 2006). These fundamental differences could collectively explain variations in associations between species. European shags association may be driven by both diving costs and prey capture; slower horizontal currents could be beneficial for the meticulous searches needed to ambush prey at close range and/or diving costs could be considerably higher in fast horizontal current speeds, even amongst particularly efficient divers such as *Phalacrocoracidae* (Heath and Gilchrist, 2010). In contrast, black guillemots associations may be purely driven by diving costs; higher water elevation or slower horizontal current speeds seem unlikely to enhance their capability to pursue prey in open water.

Other conditions

Neither black guillemots nor European shags showed relationships with sea state. Sea state was primarily included to account for its probable influence on the detectability of foraging seabirds. This result suggests that the detection of foraging seabirds in shore-based surveys may be less effected by sea state than generally believed (Jackson and Whitfield, 2014), particularly when observations are constrained to reasonable distances (< 2 km) from the vantage point (Waggitt *et al.*, 2014). It is also possible that energetic cost of dives increases in higher sea states (Finney *et al.*, 1999), which could also discourage seabirds from foraging in these conditions. Therefore, this result could also indicate that particularly high sea states (Beaufort scale > 3) are needed to influence the foraging activities of pursuit-diving seabirds in coastal environments. Higher densities of foraging black guillemots occurred during afternoon periods, whereas densities of European shags remained similar across morning and afternoon periods. Diurnal patterns of foraging activities are typically linked with the behaviour of mobile prey (e.g. diel-vertical migration: Regular *et al.*, 2010), changes in light-levels effecting the detection of prey (Regular *et al.*, 2011), or commuting distances between breeding colonies and foraging areas. However, black guillemots breed locally and probably exploit sessile benthic prey items, whereas light levels would not differ greatly between morning and afternoon

periods. Instead, the increased levels of foraging activities during afternoon periods could be an artefact of low-slack tides being primarily surveyed during this time, despite efforts being made to cover as many different combinations of tidal state and *ToD* as possible.

Occupancy patterns

Black guillemots and European shags forage primarily upon benthic and epi-benthic prey near the seabed (Wanless and Harris, 2004; Masden *et al.*, 2013; Shoji *et al.*, 2015). Sympatric species exploiting similar resources are expected to show differences in their foraging strategies to reduce levels of interspecific competition, facilitating their co-occurrence (Chase, 2011). Studies comparing the foraging distributions of sympatric species exploiting similar resources have typically focussed on differences in horizontal or vertical space use (Wilson, 2010). Results here showed that the highest densities of foraging black guillemots and European shags generally occurred at slightly different tidal states, providing rare evidence of segregation in time. These findings suggest that sympatric species exploiting similar resources, and also sharing the same horizontal and vertical space, could partly reduce levels of interspecific competition by consistently exploiting different time periods.

Tidal stream turbines

Tidal stream turbines will change environments immediately around devices, with likely consequences on the foraging activities on deep-diving seabirds. Assessing and mitigating potential impacts therefore requires an understanding of the mechanisms underlying foraging activities, allowing any changes to be predicted and accounted for in the risk assessment process (Scott *et al.*, 2014). The moderate to strong associations with lower water elevation and/or horizontal current speeds would have three main implications for assessing and mitigating potential impacts on black guillemots and European shags within the study area during breeding seasons. First, interactions between these species and moving components appear less likely during particularly high horizontal current speeds ($< 3\,ms^{-2}$). Combining this information with that on the rotation rates of moving components at lower horizontal current speeds could help to quantify the risk of collisions (Grant *et al.*, 2014). Second, foraging opportunities could increase in the reduced horizontal current speeds immediately around installations (Shields *et al.*, 2011), with periods of lower horizontal current speeds spanning across a larger proportion of the ebb-flood tidal cycle. Finally, moderating device operation during periods of lower water elevation and horizontal current speeds, perhaps limiting the rotation rates of moving components during these conditions, could help to reduce the risk of collisions. However, it needs acknowledging that habitat-use may differ across the annual cycle, particularly between breeding and non-breeding seasons (Waggitt *et al.*, in press), and comparable studies are needed to suggest effective mitigation measures during the latter.

There is a legal responsibility to assess and mitigate potentially negative impacts of tidal stream turbines on deep-diving seabirds (European Directive: 85/337/EEC). Environmental Impact Assessments (EIAs) typically involve small numbers of surveys being performed once a month for two years, with the aim of quantifying general abundances of seabirds using the development site across the annual cycle (Jackson and Whitfield, 2014).The approaches used in this study could supplement these monthly surveys by assessing the potential impacts on black guillemots and European shags in the area immediately surrounding the potential location of a device, and also suggesting appropriate mitigation measures to reduce the possibility of negative impacts. Without the need for extensive vessel-based surveys or deployments of oceanographic instruments in physically challenging environments, these approaches also allow useful information to be collected relatively cheaply and easily. For instance, recent developments in computational power and usability (Torres and Uncles, 2011) mean that hydrodynamic models are routinely used to assess energy resources, and suitable outputs would be available across most development sites (Blunden and Bahaj, 2007). However, issues concerning spatial variations in the detectability of seabirds on the sea surface (Waggitt *et al.*, 2014), in combination with the impracticality of monitoring tens of individual devices intensively over the ebb-flood tidal cycle, make shore-based surveys inappropriate for large-scale array installations in wide channels spanning several square kilometres. Nevertheless, these approaches could be applicable for single/small-scale array installations within narrow channels (Adams *et al.*, 2013). It is recommended that the approaches outlined within this study could help to assess and mitigate potentially negative impacts on pursuit-diving seabirds within such development sites.

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Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

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